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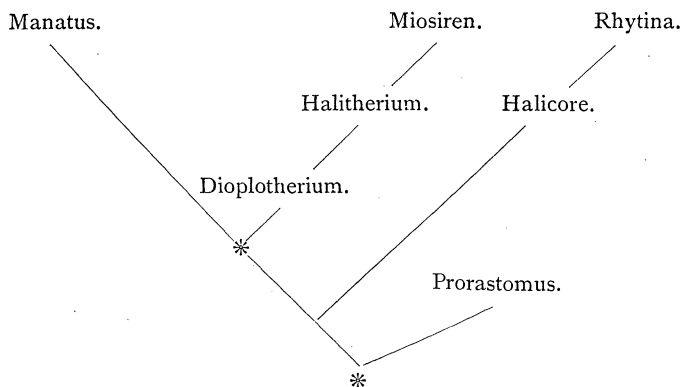
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preserved in the Museums of St. Petersburg, London, and Washington.

The lines of descent of the Sirenia may be expressed as follows:



EXPLANATION OF PLATES.

PLATE XXV.—*Diplottherium manigaultii* Cope. Three-eighths natural size. Figs. 1-4, part of premaxillary bone with incisor alveoli, and I. 1 in place; 1 outside; 2 inside; 3 front; 4 from below; *a* alveolus of external incisor. Original; from type in Museum of Charleston, S. C. Figs. 6-7, os innominatum of unknown Sirenian, from Charleston. Reduced.

PLATE XXVI.—*Halicore dugong* Cuv. Skeleton, from Cuvier.

THE CONCRESCENCE THEORY OF THE VERTEBRATE EMBRYO.

BY CHARLES-SEDGWICK MINOT.

(Continued from page 629.)

Blastodermic Vesicle with Two Layers.—Of this stage we have several descriptions; for the rabbit by Kölliker (Grundriss, p. 89), Hensen, 24, C. Rabl, 44, 141, as well as the older accounts by Bischoff, 6, and Coste, 14, and the brief mention by Heape in Foster and Balfour's Embryology, 2d edition, 316-320; for the mole by Heape, 23; for the dog by Bischoff, 7; for the cat by Schäfer, 52; for the sheep by Bonnet, 10; and for several rodents as indicated in the section on inversion of the germ layers, p. 711.

The two-layered stage is found in the rabbit about seven, in the sheep about thirteen days after coitus. The dimensions for the sheep are about 4 mm. for the greatest diameter and 2-3 mm. for the lesser diameter.

The two layers form each a closed sack; the embryonic shield is well marked as a round spot less translucent than the walls elsewhere. The outer layer has everywhere a distinctly epithelial character; in the region of the shield its cells are columnar with spherical nuclei; in the rabbit the cells are low, and the nuclei lie nearly at one level (for a good figure see Heape, 23, Pl. XXI, Fig. 49); in the sheep the cells are taller, and the nuclei are at various levels; in the mole and in various rodents there are several layers apparently, but perhaps in them also the epithelium is columnar, as it certainly is later; at the edge of the shield there is an abrupt change to a very thin layer, with widely expanded cells; consequently in the region of the shield the nuclei are close set, while outside the shield they are wider apart. The change at the edge of the shield is at first less abrupt, but at the present stage is very marked. A similar difference exists in the inner layer: although its cells are very much thinned out everywhere, yet the layer is slightly thicker in the region of the shield; the nuclei of the inner layer are everywhere somewhat flattened, and they are larger and farther apart than the nuclei of the outer layer, a difference which is very obvious in surface views, both during this and the next following stages. The inner layer has an epithelial character in the region of the shield, but further away the cells move apart, and being connected by processes resemble embryonic connective tissue (Bonnet, 10, 192; Hensen, 24, Figs. 15 and 11B on Taf. VII; E. Van Beneden, 2). The relations are illustrated by the accompanying Fig. 17, representing the shield in the sheep at thirteen days, and of a vesicle measuring 4 mm. by 2 mm.; at the left of the figure the layers are folded back over the shield.

The next changes which occur are principally those of growth, both of the vesicle as a whole and of the embryonic shield, which also begins to arch up; the vesicle and shield both become oval; usually the oval shield lies lengthwise, but in the deer, as

shown by Bischoff, it lies transversely of the vesicle. The size of the shield is quite nearly uniform among the placented mammals in which it has been studied, but the size of the vesicle varies extremely; especially noteworthy is the excessively rapid elonga-

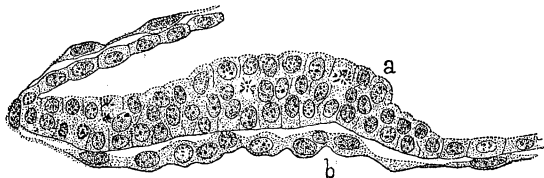


FIG. 17.—Transverse section of the embryonic shield of the blastodermic vesicle of a sheep, thirteen days pregnant, after Bonnet. *a*, outer layer of shield; *b*, inner layer of shield.

tion in ungulates (pig, sheep, goat, and deer); in the sheep, for example, it trebles or sextuples its length in less than a single day after the shield appears. The next step is the appearance of a middle layer, at least in sheep (Bonnet, 10, 192-196, 11, 42), which shows in the fresh specimen as a slight turbidity of the vesicular walls just outside the edge of the shield, while in the region of the shield there is no middle layer whatever. Sections show that the new layer consists of loosely scattered cells connected by anastomosing processes. It is everywhere absolutely distinct from the outer layer, but merges at many points with the inner layer. From this connection Bonnet concludes that the middle layer is derived from the inner layer by what must be called a process of delamination. So far as known to me, nothing analogous to this middle layer has yet been observed other mammals. The next important step, again according to Bonnet, 10, 195, is the appearance of Hensen's knot, which takes place while the peripheral middle layer is developing. The knot is at first a small thickening on the under side of the outer layer; it is situated on the middle line of the shield, a little nearer one end than the other. It is distinctly separated from the inner layer, but is connected with the cells of the middle layer, which have now developed themselves in the middle region of the shield also. Bonnet maintains that the knot gives off cells which contribute to the formation of the middle layer. The knot marks the front end of the future primitive streak.

The appearances in a sheep's ovum at this stage are illustrated by Fig. 18 of a vesicle of 12-13 days from a sheep; the vesicle measured 55 mm. in length by about 1.5 in breadth, but the length of the vesicle is extremely variable at this stage; the specimen had been stained to bring out the small close-set nuclei of the outer layer, and the larger, more widely-set nuclei of the inner layer. The upwards-arching embryonic shield, *Sh*, shows Hensen's knot, *kn*, and the beginning primitive streak, around the edge of the shield the middle layer makes an irregular shadow, *mes*.

A condition of the blastodermic vesicle similar to that described is figured by Coste for the rabbit, by Bischoff for the rabbit 6, Taf.

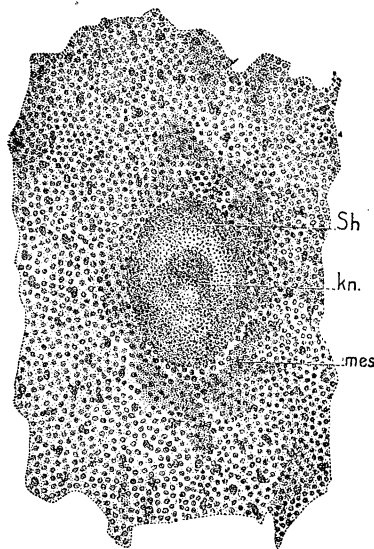


FIG. 18.—Central portion of a sheep's blastodermic vesicle of 12-13 days. *Sh*, shield; *kn*, Hensen's knot; *mes*, "Meso-blasthof"; after Bonnet, 34 diams.

ix., Fig. 42, C,—for the dog, 7, Taf. III., Fig. 28, B; and the gradual extension of the second layer is recorded for the mole by Heape, 23. Since it is known to occur in rodents, carnivora, and insectivora, it is probably true of all placental mammals that the one-layered vesicle becomes two-layered by the outgrowth of cells for the "inner mass" found at the close of segmentation; this is the first step of development after segmentation.

Rauber's Deckschicht has evidently great importance. It was first described by him in the rabbit, 45; and was also discovered by E. Van Beneden, 1, who, however, made the blunder of considering it as the permanent ectoderm, and the true ectoderm below it as the mesoderm; this error has been amply corrected by Kölliker, and is now admitted by Van Beneden (see Van Beneden and Julin, 4). Its disappearance in the rabbit has also been studied by Lieberkühn, 41. Balfour (Comp. Embryol, II., 219), from investigations on the rabbit by himself and Heape, concluded that the cells of the deck-

schicht disappear by being incorporated in the true ectodermal layer, becoming at the same time columnar; this view is verified by Lieberkühn, 42, 400-401. As already stated, the rodent modification of the deckschicht is discussed below, page 711. In the rabbit the deckschicht disappears before the second layer of cells grows completely round the vesicle.

Blastodermic Vesicles with Primitive Streak.—The knot of Hensen becomes the front end of the primitive streak, which lengthens backward; during the same period the vesicle as a whole enlarges; in ruminants the enlargement is enormous and very rapid.¹

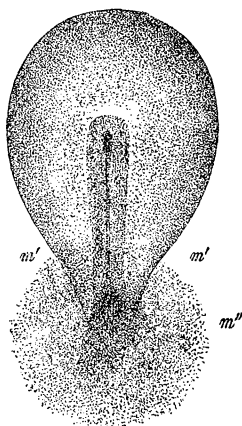


FIG. 19.—Embryonic shield of a rabbit's ovum of five days, to show the primitive streak and the distribution of middle layer, *m'*, *m''*; after Kölliker. 28 diams.

The primitive streak always lies in the long axis of the shield. The formation of the primitive streak begins with the union of Hensen's knot with the inner layer, so that at the knot all three layers are actually united,—the condition originally discovered by Hensen, 24, 268. The union of the knot with the inner layer spreads backward along the line which is to become the primitive streak; soon the axial growth reaches the edge of the shield, and the streak and shield elongate together, the latter becoming pointed at its hinder end. We thus have

a pear-shaped shield, with the primitive streak running forward from its pointed end; the anterior end of the primitive streak is somewhat enlarged, and the posterior end is considerably thickened; the three layers are united along the primitive streak. Figure 19 represents the embryonic shield of a rabbit embryo; the shield measured 1.34 mm. in length, and 0.85 mm. in width; the primitive streak is a broad band, corresponding to the axial thickening, and extends about two-thirds of the length of the shield; the middle layer, *m'*, *m''*, occupies a circular area around the hind end of the streak;

¹ Bonnet states that in the sheep the blastodermic vesicles must elongate during this period at the rate of one centimetre an hour.

for a similar stage in the opossum see Selenka, 57, Taf. XVIII., Fig. 6; in the mole, Heape, 23, Pl. XXVIII., Fig. 12; in the sheep, Bonnet, 10, Taf. x., Figs. 39, 40. Cross sections show: the concrescence of the three layers in the axis; the greater width of the streak in front (to this wide anterior end of the streak the term Hensen's knot continues to be applied); and show also the increasing thickness of the streak posteriorly. The primitive groove, which is a shallow depression of the outer layer, appears first over Hensen's knot, and thence extends gradually backward along the median line of the primitive streak. A transverse section through about the middle of the streak at this stage in the mole is represented in Fig. 20, and may be considered thoroughly typical.

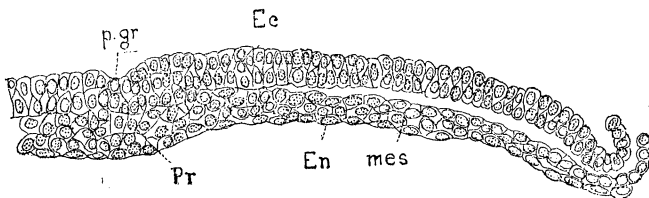


FIG. 20.—Section of the primitive streak of the mole; *p.gr.*, primitive groove; *Ec.*, ectoderm; *mes.*, mesoderm; *En.*, entoderm; *Pr.*, primitive streak; after Heape. (In sections nearer the hind end the groove *Pr.* does not appear; and the inner layer is distinct, though not separated axially from the middle layer.)

Blastodermic Vesicles with Primitive Streak and Head-Process.—

In the stage we are now considering the axial thickening becomes sub-divided into two parts, an anterior known as the head-process, (*Kopffortsatz*), and the true primitive streak. The two are distinguished by the fact that the axial thickening in the region of the process is separated from the outer layer, but fused with the inner layer, while in the region of the streak it is united with the outer layer. At this stage we find further that, except at the anterior end, *i. e.*, in the region of Hensen's knot, the axial thickening of the streak is not connected with the inner layer. Hence cross sections may give us three different appearances, according to the level at which they are taken.

The head-process was first distinguished, so far as I am aware, by Kölliker, 32, also (*Entw. ges.*, 1879, p. 271). Lieberkühn, 42,

first showed that in it appears a small longitudinal canal, the walls of which form the notochord. Heape, 23, discovered that the hinder end of this canal opens exteriorly in the mole, and Bonnet, 10, made the same observation on sheep. Strahl describes the "process" in the rabbit incidentally in his paper on cloaca, 63; additional information is given by Bonnet, 11, 65-75, concerning the sheep, and by C. Rabl, 44, concerning the rabbit. Especially valuable is Fr. Carius' dissertation, 13. In the guinea pig, according to Carius, after the formation of the primitive streak, the middle layer grows out in *all* directions, and lies free between the inner and outer layers. In front of the primitive streak the outgrowth takes place in three divisions, one median, two lateral. The median outgrowth is the head-process, and it becomes later united with the inner layer, but at first lies entirely free (embryo of 13-14 days). The first indication of the formation of a canal is an alteration of form in the cells, which elongate in directions at right angles to the axis of the head-process, so that their oval nuclei are radially placed. The change begins posteriorly and progresses forward; while it is going on, the anterior extremity of the head-process fuses with the inner layer. The radial cells move apart, so that there arises a longitudinal canal; subsequently the canal loses its inferior wall, so that it becomes continuous as a cavity with the cavity of the vesicle formed by the inner layer. In the rabbit the head-process is always free at first, but very early unites with the inner layer, in which condition it was found by Carius, 13, 18-19, at $7\frac{1}{2}$ days.² In the rabbit Hensen's knot presents at this stage a small depression (the front end of the primitive groove), into which a small plug of tissue projects up from the underlying axial thickening (Carius, Fig. 7); Van Beneden homologizes this with the anus of Rusconi and its plug of yolk matter, but inasmuch as the rabbit and bats are the only mammals known to have such a plug, and as the anus of Rusconi is necessarily at the hind end of the primitive streak, Van Bene-

² C. Rabl, 44, 143-145, states expressly that in the rabbit the axial thickening is not connected with the inner layer, either under the head-process or under the primitive streak. He differs from other investigators in this so much that I think his preparations were probably defective; indeed his own figures suggest at once that the inner layer has been artificially separated from the overlying ones.

den's homology seems to me utterly baseless. The relations of the head-process in the sheep are very much as in the rabbit, Bonnet, *II*, 65-67; the cells of the middle layer are at first free as they grow forward to form the process, but subsequently are found united with the inner layer.

The head-process (cf. Lieberkühn, 43) probably always grows, as is certainly the case in the guinea pig, at its hinder end and at the expense of the primitive streak; it is, I think, in this manner that the often-noticed shortening and final disappearance of the streak is effected. The back growth of the process establishes the necessary condition for the growth of the notochord at its hind end.

Homologies of the Mammalian Blastocyst.—There is at present no satisfactory and generally accepted interpretation of the parts of the mammalian blastocyst as compared with the corresponding stages of other vertebrates. The principal difficulties are two, namely: 1, the development of the two-layered stage; 2, the identification of archenteric cavity.

1. The two-layered stage is said to develop by an *inner* layer growing out in all directions from the inner mass of cells left at the close of segmentation. Now we must look on this statement with great suspicion, because in *all* other vertebrates it is the ectoderm which grows over the ovum; it is therefore improbable that in mammals it is the entoderm; and, in fact, I cannot find anywhere any definite observations to show that it is the inner layer the spreading of which renders the blastodermic vesicle two-layered. If the current statement proves erroneous, then we shall gain much towards a direct comparison of mammalian development with that of other vertebrates.

2. The permanent archenteric cavity arises from two sources, namely: the large space of the vesicle enclosed by the inner layer, and secondly, the so-called chorda-canal of the Kopffortsatz. Concerning the homologies of the latter, three views have been advanced: 1, it is the homologue of the tubular notochord; 2, it is the true archenteric cavity (E. Van Beneden, 3); 3, it is the blastoporic canal (Minot, 1887, Buck's Reference Handb., VI., p. 247). The third view is the one which I adopt.

Against the first view it is to be urged that the tubular stage of the notochord does not appear actually, but is assumed for lower vertebrates, because the chorda appears in them as a *groove* and as afterwards separated off, and although it is then a solid rod of cells it has been considered to represent an epithelial tube; moreover, this stage occurs after the notochord is permanently separated from the entoderm, and finally the whole of the rod of cells (or walls of the chordal tube) participates in the formation of the notochord. The mammalian "chorda-canal" is a true tube, which the notochord is not; it fuses with the entoderm, and the true notochord is separated off subsequently, only the dorsal part of its walls produces notochordal cells. These characteristics are, on the other hand, precisely those which belong to that hinder portion of the archenteron which we call in other vertebrates the blastoporic canal; this canal produces the notochordal cells from its dorsal wall; it passes through a mass of cells, and lies in Sauropsida (the vertebrates nearest the mammals) above the archenteric cavity proper. Against the second view—E. Van Beneden's—that the "chorda-canal" is the archenteron, it is to be remarked that the archenteron is bounded above by entodermal cells and below by the entodermal yolk, and the representative of the yolk is not to be found in the lower wall of the "chorda-canal." Hence it seems to me clear that Minot's view is the only defensible one, for the chorda-canal agrees in its essential features with the blastoporic canal of vertebrates, and only with that canal.

If this homology is correct then the canal must lead into the archenteron; hence the large space within the inner layer must be homologous with the archenteron, because the chorda-canal opens into it. This leaves us still entirely in the dark as to how the development of the mammalian entodermal canal is to be homologized with its development in other vertebrates.

According to the view I have advocated, the blastoporic canal of mammals is peculiar in persisting for a long time as a separate canal above the archenteron, and then losing its lower wall along a considerable stretch at once; in other vertebrates it loses in front as fast as it grows behind, so that it is always short.

As regards the homologies of the layers, I consider that the outer layer of the vesicle is ectoderm, and the thickening which constitutes the embryonic shield corresponds to the ectodermal thickening of the embryonic area in Sauropsida; the inner layer and the lining of the "chorda-canal" (blastoporic) is the entoderm; the remaining tissue of the primitive streak and head-process, together with the middle layer, constitute the mesoderm. In order not to prejudge the question, the names of the germ-layers have not been used in the preceding description of the blastodermic vesicle.

Inversion of the Germ-Layers in Rodents.—In many but not all rodents the outer layer, Rauber's Deckschicht, of the embryonic shield undergoes a remarkable hypertrophy immediately after the close of segmentation proper; the deckschicht, together with the ectoderm underlying it, becomes a plug which pushes in the other layers, thereby profoundly altering the topography of the ovum. In the mole, Heape, 23, the hypertrophy is not very great, and the plug disappears soon, so that there is no great change; in guinea pigs, mice, and Arvicola the plug becomes very large, and remains for a long time. The plug is very long, and the ovum elongates with it, changing into an almost cylindrical vesicle (Selenka's *Keimcylinder*). The plug becomes hollow, and the cells corresponding to the deckschicht become separated from those which are to form the ectoderm of the embryo. Three modifications of the hollowing out of the plug and of the separation of its two parts are known. The changes referred to are very clearly illustrated by Selenka, 56, Taf. xvi., in a series of comparative diagrammatic figures. In the simplest case, Fig. 21, the plug acquires a single cavity, *a*; the cells around the upper end, *D*, correspond to the deckschicht, and serve partly to attach the ovum to the uterine walls; the cells, *Ec*, around the lower end of the cavity become the embryonic ectoderm; all the cells around the cavity, *a*, are homologous with the outer layer of the embryonic shield of other mammals. The cavity, *c*, of the vesicle is very much reduced; the inner side of the shield, *i. e.*, of the plug, is lined by an inner layer, *en*, which gives rise to the entoderm. The outer layer of the vesicle is very thin, and is found to unite very closely

with the walls of the uterus. Hence, when the uterus is opened only the hollow plug and its covering of entoderm can be removed; as it makes a two-walled vesicle, it was considered to represent by itself the two-layered stage of the blastodermic vesicle. Thus it came that Bischoff believed that in various rodents the ectoderm lies inside, the entoderm outside. Bischoff's observations, 8, 9, which have been confirmed by Reichert, 47, are correct, but the inversion of the layers is apparent, not real. The actual

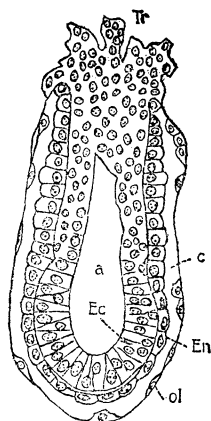


FIG. 21. — Blastodermic vesicle of *Mus sylvaticus*, after Selenka. *a*, cavity of Träger; *Ec.*, ectoderm; *c*, cavity of blastodermic vesicle; *En.*, entoderm, *ol.*, outer layer.

homologies were not discovered until the improvements in microscopic technique enabled Selenka, 55, 56, and Kupffer, 38, to make sections of uteri with ova in situ, and in their sections to find the true outer layer. Their observations removed at once the apparent anomaly in the position of the germ-layers. Their results have been in the main confirmed by Fraser, 20, and extended to another species by Biehringer, 5.

In *Mus decumanus* the ectodermal cells early become a separate spherical mass, thus dividing the plug into two parts; a cavity appears in each part; these two cavities soon become confluent, and the inner layer of cells having meanwhile developed, the relations become essentially identical with those in *Mus sylvaticus*, Fig. 21. In *Mus musculus* the development is similar, but there is the additional peculiarity that the deckschicht is regularly invaginated at first, so as to form a small pit, into which living tissue grows. In *Arvicola* this invagination is more marked and lasts longer, but in both cases it is early obliterated.

Arvicola represents the second modification mentioned above; it has not only the invagination to distinguish it, but also the very early formation of the cavity of the plug as a fissure between the deckschicht and the true ectoderm cells.

The guinea pig offers the third modification, and is characterized by the early complete separation of the plug into its two parts;

the *deckschicht* remains at one end of the ovum and forms the *träger*; it acquires an independent cavity of its own; the ectodermal portion of the plug forms a solid spherical mass, which is transported to the opposite pole of the ovum; it subsequently becomes hollowed out, presenting a space, which, as the later development shows, is the amniotic cavity. The inner layer passes from the edge of the *träger* around the sphere of ectoderm; if the two parts of the plug were connected the relations of the inner layer would be the same as in *Mus sylvaticus*, Fig. 21.

The subsequent development of the rodents with inverted layers is modified in various secondary features, which it will be unnecessary for us to study. In all typical respects the embryonic development agrees with that of other mammals, even as to details.

Blastopore.—The blastopore is the small opening which is situated at the end of the primitive streak, and leads into the archenteric cavity; the portion of the archenteron, which is next the blastopore, is a narrow passage through the thick mass of cells which make the posterior part of the primitive streak; this passage is called the blastopore canal; from its dorsal wall the cells arise which form the notochord.

While concrescence is going on the blastopore changes its position, being always at the end of the archenteron; after concrescence is completed the archenteron expands so as to extend below the primitive streak, behind the blastopore; hence the blastoporic canal appears as shown in Fig. 22, like a separate tube; it must not, however, be forgotten that it is part of the archenteron.

The blastoporic canal remains open in marsipobranchs, ganoids, amphibians, and selachians, and is well known. It is also found in all the amniota, but the recognition of its occurrence in this group was long hindered by the fact that it does not exist at first as a canal. The blastopore is the opening of a tube through the primitive streak; now if the cavity of this tube is obliterated by its walls growing together, then the primitive streak would become a solid mass of cells; this is the condition we actually find in the amniota, Fig. 22 A; since the posterior part of the primitive streak is morphologically the thick walls of the blastopore, the homologies are not altered by the temporary ob-

literation of the canal, which moreover appears as such in later stages. Its development has been especially studied in reptiles

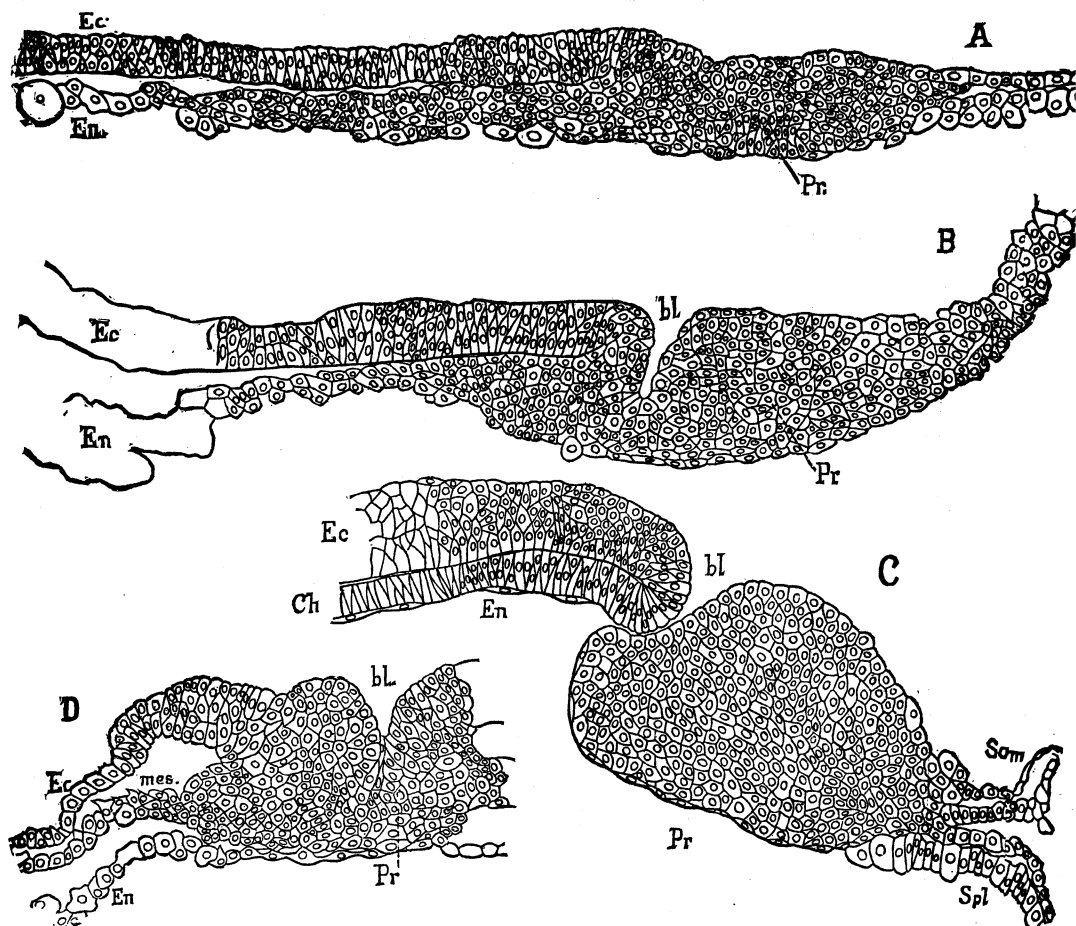


FIG. 22.—Formation of the blastoporic canal in *Lacerta muralis*, after Weldon. A, B, C, longitudinal sections of three successive stages of the blastoderm, which in each case has been removed from the yolk; the space under the entoderm, *En.*, is the archenteric cavity. D, transverse section of the posterior part of the blastopore, a little younger than C. *Ec.*, ectoderm; *En.*, entoderm, *Pr.*, primitive streak; *bl.*, blastopore; *Ch.*, notochord; *mes.*, mesoderm. Fig. B, *bl.* This pit soon becomes a complete perforation.

by Weldon, 66, Kupffer, 37, 39, H. Strahl, 58, 59, 60, 61, 62, Hofmann, in Braun Thierrich, pp. 1892-1897, and others; it begins as a pit upon the external surface.

Concrescence involves necessarily the gradual recession of the blastopore; in most vertebrates the blastoporic canal merges at its front end into the main archenteric cavity, but in mammals, if the homologies I have drawn above be correct, the canal persists for a considerable period as the "chorda-canal" of German writers.

The blastopore is not homologous with the gastrula mouth, but is merely a small portion thereof; in front of it the gastrula mouth is closed by concrescence; while concrescence is going on there will be a part of the gastrula mouth open behind the blastopore; when concrescence is completed the blastopore is at the end of the elongated gastrula mouth, the lips of which are united throughout the remainder of their length. The blastopore is not a fixed point, being merely the opening of the closed archenteron, and as by concrescence the archenteron is elongated, in precisely the same measure the blastopore travels backward.

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THE HISTORY OF GARDEN VEGETABLES.

BY E. L. STURTEVANT.

(Continued from page 646.)

SKIRRET. *Sium sisarum* L.

THIS plant seems to have been unknown to the ancients; certainly no mention can be found of an umbellifer with grouped and divergent roots, the peculiarity of the Skirret alone among European cultivated plants of this order. In the sixteenth century the name *siser* was applied to the carrot as well as to the Skirret, as by Camerarius¹ who describes *siser*, the *sisaron* of the Greeks, as a correct Skirret, and under *siser alterum*, Italian *carota bianca*, German *gierlin*, Spanish *chirivias*, French *chervy* or *girolles* or *carottes blanche*, as a carrot, and other illustrations of this period and earlier might be given. Fuchsius² in

¹ Camerarius. *Epitome*, 1586, 226, 227.

² Fuchsius. *De Stirp.*, 1542, 752.